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ON DISPERSION IN VISUAL PHOTORECEPTORS

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Abstract—An idealized visual pigment absorbance spectrum is used together with a Kramers-Kronig dispersion relation to calculate the contribution of the visual pigment to the refractive index of the fly photoreceptor. It appears that an absorption coefficient of $0.010 \mu\text{m}^{-1}$ results in a refractive index variation of less than 5×10^{-4} . The effect of this small variation on waveguide properties of the fly photoreceptor is found to be negligible. It is argued that this conclusion also holds for other visual photoreceptors.

INTRODUCTION

Visual photoreceptor structures behave as optical waveguides (Toraldo di Francia, 1949; Enoch, 1961) because the refractive index of the photoreceptive medium exceeds that of the surrounding region, and their diameter is in the order of the wavelength of light. Light conduction in the photoreceptor effectively increases the probability of light absorption in the visual pigment, and thus the overall sensitivity of the sensory cell.

At the same time, the spectral sensitivity, although determined primarily by the absorption spectrum of the visual pigment, depends on the waveguide properties. The critical parameters are the waveguide's radius and the refractive indices of the media within and outside its boundary.

In this account we wish to focus attention on a particular case of waveguide influence on spectral sensitivity. An absorbing medium always has a wavelength-dependent refractive index. This dispersion is extreme and so-called anomalous in the region of an absorption peak. Hence, the absorption in a photoreceptor caused by the visual pigment leads to anomalous dispersion in the photoreceptor waveguide. The refractive index variation influences the waveguide properties which in turn will affect the spectral sensitivity of the visual sense cell. Thus dispersion may be of importance in vision.

The effect of anomalous dispersion has been discussed recently by Snyder and Richmond (1972, 1973). They consider the absorbing molecule as a damped oscillator. The refractive index then is described by an analytic function according to classical Lorentz theory.

In the present paper the validity of this simple approach is examined. We have used a general dispersion relation and calculated the dispersion within a photoreceptor medium based on a realistic photopigment absorption spectrum. Subsequently we have quantitatively estimated the influence of the dispersion caused by the visual pigment on the spectral sensitivity of the receptor cell.

REFRACTIVE INDEX CALCULATIONS BASED ON A VISUAL PIGMENT SPECTRUM

An absorption band of a medium results in a contribution to the refractive index of the medium. The

Kramers-Kronig dispersion relation describing this contribution is presented in the appendix (equation (A4)). We have applied this relation to the absorption spectrum of an idealized visual pigment represented in Fig. 1a by the solid curve. The α - and β -band have been taken from the cattle rhodopsin-extract spectrum determined by Collins, Love and Morton (1952). These data are adjusted to the spectrum determined microspectrophotometrically by Liebman (1972) who used light polarized perpendicularly to the long axis of a frog red rod; a smooth line is drawn through these data. The latter spectrum is chosen because it covers a very broad wavelength range. The γ -band of the frog rhodopsin data is in close accordance with the corresponding data of cattle, if the latter

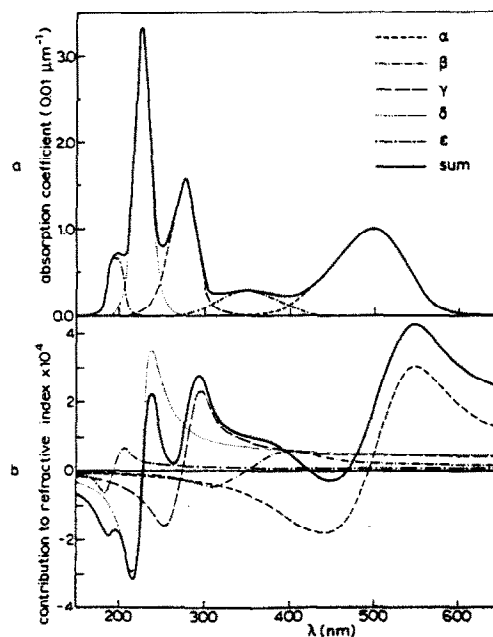


Fig. 1. Absorption coefficient (a) and refractive index (b) of idealized visual pigment. The complete spectrum is resolved in five bands, called α to ϵ . For each band the conjugated dispersion curve is calculated with the dispersion relation equation (A4). The solid dispersion curve n_p of Fig. 1b is conjugated by equation (A4) to the solid absorption curve of Fig. 1a.

are corrected for dichroism (Liebman, 1972). As shown in the figure (dashed and dotted curves), the complete spectrum is resolved into five bands.

It is well known that the absorption in the α - and β -band originates from the pigment chromophore. The other peaks most probably reflect the absorption by the protein part of the visual molecule. For convenience sake they are indicated by γ , δ and ϵ .

Although we are primarily interested in the visual region, each distinct absorption band contributes to the refractive index over the whole spectrum. To gain insight in the separate contributions we have calculated n_x , n_β , n_γ , n_δ and n_ϵ with equation (A4) from the corresponding κ_x , κ_β , etc. represented by the dashed and dotted curves in Fig. 1b. The calculations are based on a maximum absorption coefficient in the α -band given by $(\kappa_x)_m = 0.010 \mu\text{m}^{-1}$, at $\lambda_m = 498 \text{ nm}$.

Each absorption band causes a dispersion curve which is normal (i.e. decreasing with wavelength), except in the region of extreme absorption where anomalous dispersion occurs. Since equation (A4) is a linear equation, the refractive index corresponding to the full spectrum is obtained by summing the separate results. Therefore, the solid curve in Fig. 1b yields the quantitative variation in refractive index in a photoreceptive medium from the far ultraviolet up to and including the visual wavelengths.

Henceforth we restrict our interest to the visible region, i.e. α - and β -absorption bands. Clearly, the dispersion here is chiefly due to the α -band. Although the other four bands slightly counteract the variation in n_x , we still obtain in our example for the difference between the extreme values in the refractive index n_p , a value of about 4.5×10^{-4} ; n_p being the total refractive index contribution.

Next we investigate how dispersion influences the waveguide properties of photoreceptors.

THE EFFECTIVE ABSORPTION COEFFICIENT OF A PHOTORECEPTOR

Light entering an optical waveguide is propagated in wave patterns known as modes (Kapany, 1967). The relevance of the modes in vision is based on the fact that the light energy is only partly conducted within the boundaries of the photoreceptor. This fraction of power, η , is for each mode a function $\eta(V)$ of a dimensionless parameter V , defined by (Biernson and Kinsley, 1965; Snyder and Richmond, 1972)

$$V = 2\pi \frac{\rho}{\lambda} [n_1^2 - n_2^2]^{1/2}, \quad (1)$$

ρ is the radius of the circle-cylindrical fibre, n_1 and n_2 are the refractive indices of, respectively, the medium within and that surrounding the lightguide. Data for $\eta(V)$ have been presented graphically by Biernson and Kinsley (1965).

The spectral sensitivity of a visual sense cell is principally determined by the absorption in the α - and β -band. Now, in photoreceptors Beer's law holds, but with a slight though important modification. Absorption of light quanta takes place in the visual pigment which is present only within the receptor. Hence, if κ represents the absorption coefficient of the photoreceptor medium, the effective absorption coefficient

κ_{eff} equals this absorption coefficient times the fraction of light energy η propagated inside. Or

$$\kappa_{\text{eff}} = \eta\kappa. \quad (2)$$

From equations (1) and (2) it appears that η implicitly is a function of n_1 , the refractive index of the photoreceptor medium.

However, it must be noted that n_1 in turn depends on the absorption coefficient κ , as follows immediately from the preceding section. We have shown in the appendix that if κ_p represents a restricted part of the absorption spectrum, then its contribution n_p to the refractive index originating from the remaining part n_o results in the ultimate refractive index

$$n_1 = n_o + n_p. \quad (3)$$

Thus, κ_{eff} depends on the absorption coefficient of the visual pigment both directly and indirectly (via η). It is the latter, indirect action which is discussed by Snyder and Richmond as the effect of anomalous dispersion on visual photoreceptors.

THE DISPERSION EFFECT IN FLY PHOTORECEPTORS

Because of our special interest in fly photoreceptors we have treated the dispersion effect in this case in a quantitative way. It should be remembered that in compound eyes of flies two types of visual receptors or rhabdomeres are found. The slender type has a constant radius of about $0.5 \mu\text{m}$ along its entire length. The wider one tapers from distal to proximal from about 1.0 to $0.5 \mu\text{m}$ (Boschek, 1971). The refractive indices of waveguide and surrounding medium are taken to be $n_o = 1.360$ and $n_2 = 1.339$, respectively (cf. Stavenga, 1974).

In order to obtain in detail the effect of dispersion at different waveguide radii all calculations are carried out with four values of ρ ranging from 0.4 to $1.0 \mu\text{m}$. First, dispersion is neglected, i.e. $n_1 < n_o$. After calculating V as a function of wavelength, the fraction of the light power propagated inside the photoreceptor then may be determined from the function $\eta(V)$. The solid curves in Fig. 2 thus represent the light-power fraction, denoted by η_o , in the unperturbed, dispersionless situation, as a function of wavelength.

Subsequently we have introduced dispersion. Now, an accurate absorption spectrum of fly visual pigment is not yet at our disposal. However, our measurements on the photopigment of the fly *Calliphora erythrocephala* M. (Stavenga, Zantema and Kuiper, 1973) reveal that the absorption spectrum may be approximated by the spectrum of the idealized pigment used before. Together with an upper estimate for the absorption coefficient in the fly of $0.010 \mu\text{m}^{-1}$ we can use the resulting dispersion n_p from Fig. 1b as obtained from Fig. 1a. The perturbed V then is obtained from these data with equations (1) and (3). The resulting light fraction η , represented by the dashed curves in Fig. 2, is seen to differ but little from the unperturbed η_o .

Finally we wish to discuss the influence of the dispersion on the effective absorption. Again we have

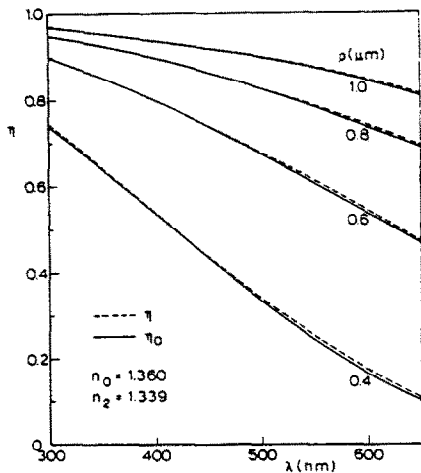


Fig. 2. The light-power fraction propagated inside an optical waveguide as a function of wavelength in fibres with different radii ρ . The unperturbed fraction η_0 is obtained when the medium of the waveguide exhibits no dispersion and the refractive indices of the waveguide and surrounding medium are respectively $n_0 = 1.360$ and $n_2 = 1.339$. If the substance possessing the dispersion of Fig. 1b becomes a constituent of the waveguide medium then the perturbed fraction η is obtained. η_0 and η are represented by the solid and dashed line, respectively.

compared the unperturbed and the perturbed case or

$$\kappa_{eff}^0 = \eta_0 \kappa_p \quad \text{and} \quad \kappa_{eff} = \eta \kappa_p. \quad (4)$$

Figure 3 represents the absorption by the chromophoric group, $\kappa_z + \kappa_\beta$. Multiplication by η_0 results in the unperturbed absorption coefficient κ_{eff}^0 (solid lines), while using η the perturbed absorption coefficient κ_{eff} arises (dashed lines). For clarity's sake only the cases with $\rho = 0.4 \mu\text{m}$ and $\rho = 0.8 \mu\text{m}$ are given.

It is obvious that the effect of the dispersion originating from the visual pigment is not at all dramatic. However, there is quite another significant feature to be observed, viz. the effect of the radius: the absorption peak in the slender waveguide is shifted

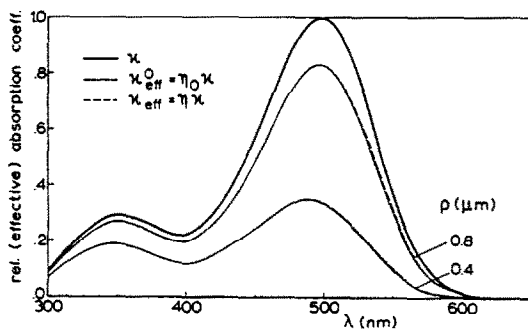


Fig. 3. The effective absorption coefficient of a visual photoreceptor. The absorption coefficient of the photoreceiving medium, is multiplied with η_0 and η (shown in Fig. 2) for the cases $\rho = 0.8 \mu\text{m}$ and $\rho = 0.4 \mu\text{m}$. The resulting effective absorption coefficient of the visual waveguide, κ_{eff}^0 and κ_{eff} respectively, are virtually equal. κ_{eff} and κ_{eff}^0 are smaller in the slender than in the wider waveguide. Moreover, they are progressively shifted towards shorter wavelengths.

with regard to that in the wider one (cf. Snyder and Pask, 1973a). This shift towards shorter wavelengths is counteracted very slightly by the dispersion effect as follows from comparison of κ_{eff}^0 and κ_{eff} .

So, we have to conclude that the effective absorption spectrum of a fly photoreceptor certainly can deviate from the absorption spectrum of the pigment localized in it. However, this change is almost exclusively the consequence of a general property of optical waveguides, namely that a wavelength dependent fraction of the light energy is propagated outside its boundary. The action of anomalous dispersion must be, at least in the fly, of very minor importance.

DISCUSSION

Starting with the absorption spectrum of an idealized visual pigment in a photoreceptor we have calculated the dispersion originating from the pigment.

An obvious proviso to be made concerns the approximation of fly visual pigment by cattle rhodopsin. Since all invertebrate visual pigments studied so far appear to be rhodopsins, i.e. vitamin A₁-based (Goldsmith, 1972), this conjecture seems permissible. The most important figure is the extreme value of the absorption coefficient of the pigment. Accepting $0.010 \mu\text{m}^{-1}$ as a certainly extreme value Fig. 2 shows that at all rhabdomere cross-sections the waveguide properties undergo a vanishing influence of the dispersion. Application of the value derived for the housefly by Kirschfeld (1969) being $\kappa_z(\lambda_m) = 0.005 \mu\text{m}^{-1}$ results in an even smaller effect.

It should be remarked that Fig. 2 is based on refractive index values deviating from those determined experimentally by Seitz (1968). He reported for the rhabdomere medium a refractive index of 1.349 and for the two media bordering the rhabdomere, values of 1.341 and 1.3365 respectively. However, the measurements of Seitz must have been influenced by waveguide effects (Stavenga, 1974, 1975). After correction adequate values are $n_1 = 1.365 \pm 0.006$ and $n_2 = 1.339 \pm 0.002$. In the present investigation we have taken $n_0 = 1.360$ to avoid a possible underestimate of the effect of anomalous dispersion on absorption. Yet, it can be seen readily that even with $n_0 = 1.349$ the resulting effect remains negligible.

In Fig. 3 we have presented the effective absorption coefficient for the case of circle-cylindrical photoreceptors. Actually the peripheral fly rhabdomeres taper, however. In tapering optical waveguides the light-power fraction η and accordingly also the effective absorption coefficient are a function of the longitudinal coordinate. Integration along this coordinate then yields the total absorption (Snyder and Pask, 1973b,c). This reveals that also in the case of the tapering fly rhabdomeres the dispersion effect is negligible, which outcome is comprehensible with regard to Figs. 2 and 3 where it is shown that in the actual radius range of 0.5–1.0 μm the influence of dispersion is very small.

Yet we have to mention that the light intensity entering a waveguide depends on wavelength and on the waveguide parameters: radius ρ and refractive indices n_1 and n_2 . The light-entrance function can be approximated by $\eta(\lambda)$ (Snyder and Richmond, 1972, 1973). In a fly rhabdomere the radius value at the

distal end is $1.0\ \mu\text{m}$. In Fig. 3 the vanishing dependence of η on dispersion at this radius value is shown. After all we thus can but conclude that dispersion will affect the extinction spectrum of fly rhabdomeres very inconspicuously indeed.

As is revealed by Fig. 3, the only change in the effective absorption coefficient of fly rhabdomeres to be observed in practice is the shift towards shorter wavelength as a consequence of a small radius. Since both types of rhabdomeres contain the same visual pigment (Stavenga *et al.*, 1973) the blue shift in the slender one is supposed to be essential in the fly colour-vision system (Snyder and Miller, 1972; Snyder and Pask, 1973a; Stavenga *et al.*, 1973).

Of particular interest to our discussion is Snyder and Richmond's quotation of the average extinction curve of fly photoreceptors, measured microspectrophotometrically by Langer and Thorell (1966). They explain the bumpiness of this curve with the effect of anomalous dispersion. We discard this and point to an entirely different interpretation (see the comment added by Langer to Stavenga *et al.*, 1973).

Our photochemical studies on the visual pigment of the fly have shown that the visual molecule does not decompose after quantum absorption. In contrast with vertebrate pigments, a thermostable photoproduct is created. It has become apparent now that the microspectrophotometric curves cited by Snyder and Richmond do not represent the pure visual pigment but are obtained from mixtures of native pigment and photoproduct.

Having arrived at this point we can ask what the rather involved Kramers–Kronig approach which we have presented here, has improved on the much simpler Lorentz treatment given by Snyder and Richmond (1972). In answer to this question we have developed in the appendix some useful relations. Dealing with a single Lorentzian absorption peak the resulting extreme deviation in refractive index equals [see the appendix, equation (A9)]

$$\Delta n = \frac{\kappa_m}{4\pi} \lambda_m \left[1 - \left(\frac{\sigma}{2} \right)^2 \right] \quad (5)$$

where κ_m is the maximal absorption coefficient, at wavelength λ_m and $\sigma\lambda_m$ the distance between the two wavelengths where the absorption coefficient is at half the maximal value. Approximating the visual pigment α -band with a Lorentzian yields $\sigma \approx 0.2$ (and not $\sigma \approx 0.1$ following Snyder and Richmond, 1972). With $\lambda_m = 0.498\ \mu\text{m}$ and $\kappa_m = 0.010\ \mu\text{m}^{-1}$ equation (5) yields $\Delta n \approx 4.0 \times 10^{-4}$. We have noted above that according to Fig. 1b the difference between the extreme refractive index values is 4.5×10^{-4} even when including involvement of the counteracting effects of the β , γ , etc. bands. So the dispersion effect in the approximated treatment is yet slightly smaller than in the elaborately discussed accurate approach which already yielded vanishing effects.

Still more, equation (5) provides us with the possibility to study quickly the case of vertebrate photoreceptors. Here the maximal absorption coefficient κ_m can amount up to about $0.04\ \mu\text{m}^{-1}$ (Liebman, 1973). Assuming a visual (cone) pigment peaking at $\lambda_m = 0.55\ \mu\text{m}$ the variation in refractive index then becomes approximately $\Delta n = 1.8 \times 10^{-3}$. To establish the influence of this refractive index change we

have to compare this value with the difference in refractive indices of the media inside and outside the visual photoreceptor $n_1 - n_2$. In vertebrates $n_1 - n_2$ values about 0.05 – 0.07 (Barer, 1957). The variation in $n_1 - n_2$ induced by dispersion amounts to at the utmost 4 per cent. This is about twice the variation calculated in the case of the fly rhabdomeres: $4 \times 10^{-4}/0.021 \approx 2$ per cent. Hence, it can be concluded that also in vertebrate visual photoreceptors the influence of dispersion is small, which conclusion also emerges from explicit calculations using the Kramers–Kronig relation. So the spectra produced by Marks, Dobelle and MacNichol (1964) (obtained from partly bleached primate cones!) which are cited by Snyder and Richmond (1972, 1973) as an instance of influence by anomalous dispersion have to be explained in other terms (for a critical review we refer to Liebman, 1972).

As a general remark we wish to state that we principally agree with the concepts of Snyder and Richmond concerning the influence of dispersion on optical waveguide properties. With the introduction of the Kramers–Kronig relation we have merely refined their theory. Yet, because Snyder and Richmond have taken into account the α -band only, and furthermore have failed to apply reasonable values for the absorption coefficient, they erroneously have found examples of "undoubted changes in extinction resulting from anomalous dispersion" (Snyder and Richmond, 1972, 1973).

In conclusion we claim that the dispersion in the visual photoreceptors is of minor importance to the visual process.

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APPENDIX

The refractive index $n(\omega)$ of a medium and the absorption coefficient $\kappa(\omega)$, i.e. the relative light-intensity loss per unit length, are related by the Kramers–Kronig dispersion relation (cf. Bell, 1967; Stern, 1963)

$$n(\omega) - 1 = \frac{c}{\pi} P \int_0^\infty \frac{\kappa(\omega')}{\omega'^2 - \omega^2} d\omega' \quad (\text{A1})$$

where c is the wavelength in vacuum and P denotes the principal value of the integral. Since frequency ω and vacuum wavelength λ are related by $\omega = 2\pi c/\lambda$ equation (A1) is equivalent to

$$n(\lambda) - 1 = \frac{1}{2\pi^2} P \int_0^\infty \frac{\kappa(l)}{1 - \left(\frac{l}{\lambda}\right)^2} dl. \quad (\text{A2})$$

Here κ represents the complete absorption spectrum. If κ_p represents a restricted part of this spectrum and κ_o the remaining part, or

$$\kappa = \kappa_o + \kappa_p \quad (\text{A3})$$

then

$$n_p(\lambda) = \frac{1}{2\pi^2} P \int_0^\infty \frac{\kappa_p(l)}{1 - \left(\frac{l}{\lambda}\right)^2} dl \quad (\text{A4})$$

is the contribution to the refractive index originating from the absorption band(s) characterized by κ_p . Clearly from

$$n = n_o + n_p \quad (\text{A5})$$

it follows with equations (A2)–(A5) that the refractive index n_o is related to κ_o in a manner similar as given in equation (A2).

As a special example of equation (A4) we now consider briefly the classical Lorentz case.

In the Lorentz theory of absorption n_p and κ_p are derived directly (cf. Snyder and Richmond, 1972). It follows that

$$\kappa_p(\lambda) = \kappa_m \left(1 + \left[\frac{\lambda^2 - \lambda_m^2}{\sigma \lambda \lambda_m} \right]^2 \right) \quad (\text{A6})$$

and

$$n_p(\lambda) = \frac{\kappa_m}{4\pi} \lambda_m \sigma \lambda^2 (\lambda^2 - \lambda_m^2) / ([\lambda^2 - \lambda_m^2]^2 + \sigma^2 \lambda^2 \lambda_m^2) \quad (\text{A7})$$

where κ_m is the maximal absorption coefficient, at wavelength λ_m .

It can be shown that equation (A6) substituted in equation (A4) yields equation (A7).

Since at

$$\lambda_{1,2} = \lambda_m \left\{ \sqrt{1 + \left(\frac{\sigma}{2}\right)^2} \pm \frac{\sigma}{2} \right\}$$

the absorption coefficient is at half of the extreme value it follows

$$\sigma = \frac{\lambda_2 - \lambda_1}{\lambda_m}. \quad (\text{A8})$$

So σ is the relative halfwidth of the Lorentzian absorption curve.

The resulting refractive index has extrema at $\lambda = \lambda_m / \sqrt{1 \pm \sigma}$ where $n_p = \pm \kappa_m \lambda_m / (4\pi [2 \mp \sigma])$; (cf. Snyder and Richmond, 1972).

Hence, the extreme variation in the refractive index is

$$\Delta n = \frac{\kappa_m}{4\pi} \lambda_m \left[1 - \left(\frac{\sigma}{2}\right)^2 \right]. \quad (\text{A9})$$

The latter relation can be used for a quick estimation of the effect of anomalous dispersion (see Discussion).